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VOLUME 24 MAY, 1938 NUMBER 5

PROCEEDINGS

OF THE

NATIONAL ACADEMY OF SCIENCES

OF THE

UNITED STATES OF AMERICA

MAY 20 1938

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PUBLISHED MONTHLY

Publication Office: Mack Printing Company, Easton, Pa.

Editorial Office: Harvard School of Public Health, Boston 17

Home Office of the Academy: Washington, D. C.

...red as second-class matter June 21, 1920, at the post-office at Easton, Pennsylvania, under the act of August 24, 1912.
...ted for mailing at a special rate of postage, provided for in section 1103, act of October 3, 1917. Authorized June 18, 1920.

Price per annum, $5.00

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PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES
Volume 24 May 15, 1938 Number 5
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RELATIVE NUMBERS OF OPERATORS AND SUBGROUPS OF A FINITE GROUP

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Communicated March 19, 1938

Operators and subgroups are the fundamental constituents of a group. The former are commonly called the elements of a group while the latter furnished the first important entering wedge into the theory of groups when J. L. Lagrange (1736–1813) proved that the order of the symmetric group of every given degree is divisible by the order of each of its subgroups. Sometimes the number of operators of a given group is larger than the number of its subgroups if by subgroup we mean a proper subgroup, that is, a subgroup which is neither the identity nor the group itself. The term subgroup will be used with this meaning throughout the present article. It is evident that in every group of finite order the number of operators exceeds the number of its cyclic subgroups since an operator of highest order of such a subgroup cannot appear in any cyclic subgroup of the same order besides the one which it generates. In particular, every cyclic group involves more operators than subgroups.

An elementary category of groups in which the number of operators of each group is always less than the number of its subgroups is composed of the abelian groups of order 2^m, $m > 2$ and of type 1^m. In fact, the number of the subgroups of index 2 in such a group is equal to the number of its operators of order 2 according to a well-known theorem. In the special case when $m = 3$ this group contains 8 operators and 14 subgroups. It is easy to verify that every other group whose order is less than 16 contains at least as many operators as subgroups. In the dihedral group of order 2^m the number of subgroups is readily found to be equal to $2^m + m - 3$. Hence the number of its subgroups is equal to the number of its operators when $m = 3$ but for all larger values of m the number of subgroups exceeds the number of operators. We proceed to consider the relative numbers of the substitutions and subgroups in the symmetric group of degree n.

It is easy to verify that the symmetric group of degree 4 contains 28 subgroups while it contains only 24 substitutions. To prove that the

symmetric group of degree $n > 4$ contains more subgroups then substitutions it is therefore only necessary to prove that the symmetric group of degree n must have this property whenever the symmetric group of degree $n - 1$ has it. Since the number of the subgroups and of the substitutions of degree $n - \alpha$ which appear in the symmetric group of degree n is n/a times the numbers of these subgroups and substitutions in the symmetric group of degree $n - 1$ and the number of the subgroups of degrees 2 or 3 in any symmetric group is then equal to the number of the substitutions of these degrees, respectively, the theorem in question will be proved if we can prove that the number of the subgroups of degree n in the symmetric group of degree $n > 4$ is at least equal to the number of substitutions of this degree increased by one.

From the fact that if the number of subgroups in the symmetric group of degree $n - \alpha$ exceeds the number of the substitutions in this symmetric group it results that the number of the subgroups of degree $n - \alpha$ in every larger symmetric group exceeds the number of its substitutions of this degree by a number which is at least equal to the degree of the symmetric group. This results directly from the well-known number theory theorems that the product of any k successive positive numbers is divisible by $k!$ and exceeds by at least k the product of any $k - 1$ successive positive numbers divided by $(k - 1)!$ whenever the smallest of these successive numbers exceeds unity and $k > 1$. In particular, from the fact that the number of subgroups of degree 4 in the symmetric group of this degree exceeds by 4 the number of its substitutions it results directly that the number of the subgroups of degree 4 in the symmetric group of degree $n > 4$ is at least $4n$ times the number of its substitutions of degree 4.

The symmetric group of a prime degree p contains more substitutions of order p than subgroups which separately involve an invariant subgroup of order p or are themselves of this order. The number of the latter is equal to the number of the different divisors of $p - 1$, including the identity and $p - 1$, multiplied by $(p - 2)!$, while the number of the substitutions of order p is $(p - 1)!$. This symmetric group contains a large number of subgroups of degree p which do not involve a substitution of degree p. In fact, every symmetric group of degree n contains subgroups of degree n which do not separately involve substitutions of this degree whenever n exceeds 4. Such groups are necessarily intransitive since every transitive group of degree n is known to contain at least $n - 1$ substitutions of this degree in view of the fact that the average number of letters in all of its substitutions is $n - 1$. The groups of degree 5 which involve no substitution of this degree are formed by establishing a 3,1 isomorphism between the symmetric group of degree 3 and the regular group of degree 2.

The number of these groups is 10 since the symmetric group of degree

5 contains 10 symmetric groups of degree 2. If a group of degree 6 does not involve a substitution of this degree it contains three transitive constituents of degree 2 and hence it is of order 4 and is invariant under the group of degree 6 and of order 48. There are therefore 15 such groups in the symmetric group of degree 6. From the two given categories of groups it follows directly that every symmetric group of degree $n > 4$ contains groups of degree n which do not separately contain substitutions of this degree since we can readily form direct products which have this property and involve one of the given groups in each case. In particular, the symmetric group of degree $p > 3$ contains more subgroups which either involve separately a cyclic subgroup of order p or involve no substitution of degree p but have transitive constituents of degree $p - 2$, 2 as it has substitutions of degree p. That is, the symmetric group of prime degree $p > 3$ contains more than $(p - 1)$ subgroups which separately either involve invariantly a subgroup of order p or have two transitive constituents of degrees $p - 2$, 2, respectively, and involve no substitution of degree p.

To complete a proof of the theorem that the symmetric group of degree n contains more subgroups than substitutions whenever $n > 3$ it remains only to consider the group which contains a cyclic substitution of degree n when n is not a prime number since to all other cases we can apply the theorem that there are more subgroups than substitutions of degrees less than n. This results from the fact that the substitutions and the subgroups of such degrees are contained in the direct products of substitutions and of groups of lower degrees. It may also be noted that in the groups obtained by extending a cyclic group of degree $n - 2$ by substitutions on these letters which transform it into itself and by making the holomorph thus obtained isomorphic with the group of degree 2 by dimidiation, the substitution of degree n and of order less than $n - 2$ need not be considered since they appear in direct products of groups whose constituents are all of a lower degree than $n - 2$. Hence there results the theorem that *every symmetric group whose degree exceeds 3 contains more subgroups than substitutions.*

It was noted above that the number of the subgroups of the abelian group of order 2^m and of type 1^m exceeds the number of its operators whenever $m > 2$. It may be noted that in the abelian group of order p^m and of type 1^m the number of operators exceed the number of subgroups for every given value of m provided the prime number p exceeds an arbitrary given number. This results directly from the well-known formula for the number of these subgroups since the power of p in the numerator is larger than in the denominator whenever the subgroups are proper subgroups. For instance, when $p = 3$ and $m = 3$ there are 26 subgroups and 27 operators, but for larger values of m the number of subgroups exceeds the number of operators when $p = 3$.

MINIMUM DEGREE OF SUBSTITUTIONS OF HIGHEST DEGREE IN A GROUP

BY G. A. MILLER

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Communicated April 15, 1938

If a substitution group G of degree n has k transitive constituents then it involves at least one substitution whose degree exceeds $n - k$ since the average number of letters in all of its substitutions is $n - k$ and the identity involves no letters. The maximum value of k is $n/2$ and when k has this value each of the transitive constituents of G is of degree 2 and G is abelian. When n is odd the maximum value of k is $(n - 1)/2$ since at least one of the transitive constituents is then of odd degree and this degree is at least as large as 3. As G contains at least one substitution whose degree exceeds $n - k$ the minimum value of the degree of its largest substitutions is $n/2 + 1$. When the largest degree of a substitution of G is $n/2 + 1$ then all the transitive constituents of G are of degree 2 and $n/2$ is odd since this largest degree must be even. That is, *when a substitution group of degree* n *involves a substitution of degree* $n/2 + 1$ *but no substitution of a larger degree then* $n/2$ *is odd and each of the transitive constituents of the group is of degree* 2.

To construct such a system of substitution groups let n be of the form $2^m + 2^{m-1} + \ldots + 2$ and hence $n/2 + 1 = 2^m$. When $m > 1$ the group generated by a substitution of order 2 and of degree 2^m is extended by a substitution of order 2 and of degree 2^m which has 2^{m-2} of its cycles of order 2 in common with the preceding substitution. There results a group of order 4 and of degree $2^m + 2^{m-1}$ which involves only substitutions of degree 2^m besides the identity. It should be noted that there are three sets of 2^{m-2} cycles which always appear together in these three substitutions whenever such a substitution involves one of them. When $m > 2$ this group of order 4 is extended by a substitution of degree 2^m which has 2^{m-3} cycles in common with each of the given three sets of 2^{m-2} cycles. Thus there results a group of order 8 which contains seven sets of 2^{n-3} cycles which always appear together and involves only substitutions of degree 2^m besides the identity.

When $m > 3$ this process can be continued until the given sets of cycles are composed separately of a single cycle. It therefore results that whenever n is of the form $2^m + 2^{m-1} + \ldots + 2$ there is an abelian group of degree n whose substitution of largest degree is of degree $n/2 + 1 = 2^m$ and whose order is 2^m, which involves only substitutions of degree 2^m besides the identity. This group contains the same number of substitutions of every degree as the regular abelian group of order 2^m and of type 1^m and it coincides with this regular group when $m = 1$ and only then.

Each of its letters appears in exactly one-half of its substitutions. In general, the order of G cannot be less than $n/2 + 1$ since it must involve at least $n/2$ substitutions of degree $n/2 + 1$ in order to bring the average number of letters to $n/2$ on account of the identity, because the degree of no substitution can exceed the average degree by more than one.

When the order of G is $n/2 + 1$ then G belongs to the system of groups defined above since each of its substitutions besides the identity is then of degree $n/2 + 1$. Hence each of these $n/2$ substitutions has then exactly half of its letters in common with every other one. If we start with such a substitution the second substitution can be selected in essentially only one way and the same remark applies to every additional generator whenever the generators of a proper subgroup have been found. It should be observed that each of the successive generators are thus selected in such a manner that the group generated by it and the preceding generators is of the largest possible degree. Every G in which the substitution of highest degree is of degree $m/2 + 1$ is generated by its substitutions of highest degree since each of the substitutions which is not of highest degree involves less than the average number of letters of the substitutions of G. In particular, the substitutions of degree $n/2 + 1$ are positive.

Suppose now that the order of G exceeds $n/2 + 1$ and select an arbitrary substitution s of G which is of degree $n/2 + 1$. Consider the set of all the substitutions of G which have the property that their products into s are all of degree $n/2 + 1$. The number of these substitutions exceeds $n/2$ since G involves at least two substitutions whose degrees are less than $n/2 + 1$. Not more than $n/2 - 1$ of these substitutions can be of degree $n/2 + 1$ for if more than $n/2 - 1$ would be of this degree then at least two of them would have the same half of their letters in common with s while their other letter would be different from those in s. The product of these three substitutions would have a larger degree than $n/2 + 1$, which is impossible.

For each of the remaining substitutions of the given set there would be more than one substitution in G of degree $n/2 + 1$, since a substitution of degree $n/2 - 1$ would be negative, while the product with s would give only one such substitution. As this is impossible it has been proved that *a necessary and sufficient condition that there is a group of degree* n *such that its substitution of largest degree is of degree* $n/2 + 1$ *is that* n *is of the form* $2^m + 2^{m+1} + \ldots + 2$ *and there is one and only one such group for an arbitrary given value of* m. All the substitutions of this group besides the identity are of degree $n/2 + 1$. There is therefore one and only one group whose order is a given power of 2 which has the property that it can be represented as a substitution group of degree n whose substitution of largest degree is $n/2 + 1$. The degrees of these groups are 2, 6, 14, etc.

It has been noted that when the degree n of G is odd then its substitu-

tions of largest degree cannot have a degree which is less than $n/2 + 3/2$ and it is easy to see that when $n = 3$ the symmetric and the alternating groups involve such substitutions and when $n = 5$ there is a group of order 6 whose transitive constituent groups are of degrees 2 and 3, respectively, and whose substitutions of largest degree are of degree 4. By means of what precedes it is easy to prove that these three groups are the only ones whose substitutions of largest degree are of degree $n/2 + 3/2$. Such a group involves one and only one constituent group of degree 3 and the other constituent is an isomorphism between groups of degree 2. As the order of the latter constituent exceeds 2 when $n > 5$ its substitution of largest degree is at least $\frac{n-3}{2} + 1$ and the substitution of largest degree in G is therefore greater than $n/2 + 3/2$.

MEASUREMENTS OF RESISTANCE AND CAPACITY OF MONOFILMS OF BARIUM STEARATE

By C. E. Buchwald, D. M. Gallagher, C. P. Haskins, E. M. Thatcher and P. A. Zahl

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Communicated March 24, 1938

In the course of a study of the modification of surfaces formed from barium stearate monolayers by superposed films composed of less than a single complete layer of molecules, undertaken at the suggestion and with the help of Dr. Irving Langmuir, it became desirable to make some rather careful measurements of the electrical resistance and capacity of barium stearate monolayers. This work has proven sufficiently interesting and suggestive as to be worthy of preliminary announcement at this time. Further work is in progress, and a more complete paper will be published shortly.

Attempts were at first made to measure electrical resistance of barium stearate monofilms by direct means, using for this purpose electrodes consisting of heavily chromium plated and polished brass slides upon which the films were mounted by standard dipping methods. Both electrodes were coated with the number of films to be measured, and were immersed in dilute copper sulfate as electrolyte, the cell thus formed being inserted in the arm of a d. c bridge of conventional design. It was found that polarization effects were of such magnitude as to render such a method nearly valueless.

Recourse was next had to alternating current methods. A cell of the design described above was made a part of a conventional a. c. bridge network, 0.25 volts at 1000 cycles being impressed across the electrodes, and resistance and capacity measurements being recorded together. This arrangement, although workable, was undesirable in several respects. For mathematical reasons involved in the calculation of a. c. networks, it

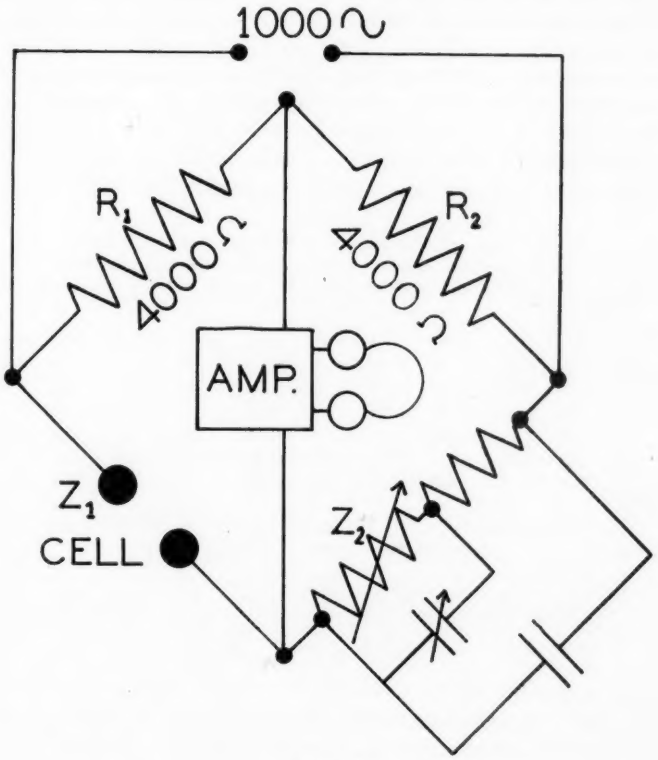

FIGURE 1

proved impracticable to obtain absolute readings for either resistance or capacity from the set, and the curves obtained showed a modification of shape which could be accounted for on grounds entirely apart from the structure of the films. Further, the form of the electrodes was not satisfactory, the chromium plating at the edges presenting sufficiently roughened surfaces so that it is highly probable that the first or subsequent layers showed irregularities or "holes" in these areas—a condition which

we have shown to be fatal to accurate measurement, since each "hole" acts as an extremely wide-mouthed potential funnel. Further, it was undesirable that the current density should be highly variable over the surfaces of the films, as it clearly must be where edges and corners are present in the electrode.

For these reasons, the arrangement finally adopted for measurement was somewhat different. The network used is indicated in figure 1. It will be seen that the circuit used constitutes a standard a. c. bridge, with the exception that an auxiliary circuit, involving a variable capacity and resistance, has been introduced into the arm Z_2. This allows a preliminary balancing of the bridge against the *unfilmed* cell chromium $CuSO_4$-chromium, and, as we shall indicate in detail in a later paper, permits direct determination of the capacity and resistance of the films laid down. As in the earlier bridge, of which this was a modification, 0.25 volts were

TABLE 1

RESISTANCES AND CAPACITIES OF BARIUM STEARATE FILMS

(These values and those shown in figure 2 are given as direct readings with both electrodes filmed. The capacities for single layers are double and the resistances one-half of the values given.)

NO. OF LAYERS	RES.	CAP. μ	RES.	CAP. μ	RES.	CAP. μ	RES.	CAP. μ	RES.	CAP. μ
1 (B)	10	6.84	16	6.42	11	6.73	23	2.71	19	2.82
3	46	3.98	51	3.99	51	3.97	42	3.33	49	3.41
5	96	2.79	92	2.98	99	3.01	71	3.02	89	2.07
7	176	2.01	193	2.07	184	1.58	101	2.71	208	1.42
9	261	1.61	271	1.53	273	0.99	132	2.15	381	0.93
11	390	1.26	403	0.97	392	0.86	239	1.40	489	0.71
13										
15	931	0.896	807		730	0.58			834	0.52
17										
19										
21	1581	0.501	1350	0.381	1353	0.39	801	0.560	1299	0.390
31	2731	0.315	2501	0.263	2638	0.234	1811	0.251	2108	0.304
41	3710	0.218	3612	0.198	3920	0.109	2847	0.151	3112	0.241

impressed across the cell at 1000 cycles. Current density was therefore low throughout the cell, a feature highly to be desired in guarding against film modification or rupture during the measurements. Standard General Radio and Leeds and Northrup variable precision condensers, backed by a battery of fixed standard condensers of I mfd. capacity, and standard Leeds and Northrup variable resistances were used in the balance arms. A storage battery was used as the voltage source, and readings were made with head phones, a 1000 cycle oscillator being used. Voltage wave-form and amplitude were checked continuously with a Type TMV-122-B R.C.A. cathode ray oscillograph.

The design of electrode finally adopted consisted of a cylindrical brass rod, 1 centimeter in diameter and 30 centimeters long, heavily and uni-

formly chromium plated and thoroughly polished. The end of the rod was of the form of a hemisphere, and was so joined to the cylinder that no discontinuities of surface whatever were presented. There was thus made available a surface upon which monofilms might be mounted which presented no sharp edges, corners or discontinuities, and from which water might drain evenly when dipping. The electrodes were separated by suitable bakelite collar mountings, were both filmed as before, and were mounted, as before, in an electrolyte bath of 0.35 M $CuSO_4$. Connection was made with the electrodes by means of spring clips.

A standard Langmuir tray was used for preparing the films. The bath contained 100 mgm. $BaCl_2$, .6 H_2O in 4450 cc. distilled H_2O and was

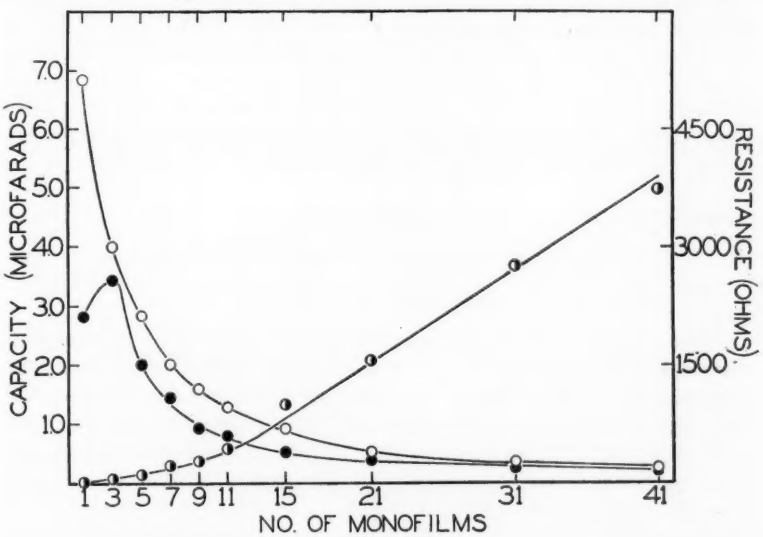

FIGURE 2

of pH 7.31. Stearic acid, from a solution of 142 mg. stearic acid in 40 cc. of redistilled benzene, was spread in standard fashion; oleic acid being used as piston oil. The electrodes were dipped by hand, and dipping was done with extreme care, as the slightest imperfection in the first B film proved serious.

The results are shown in table 1. Here are listed the resistances and capacities of varying numbers of film layers for five sets of runs. It will be noticed that in three of these runs the highest value for the capacity is shown for the initial (B) layer. For the remaining two, the layers deposited on the *second* dip (total, BAB) show a higher capacity value than does the original B. This anomaly has been studied rather carefully, and

it has been found that, when a peak of capacity thus occurs, the capacity values for numbers of layers greater than three are atypical. This is shown rather clearly in figure 2. Here are plotted the values for the resistance and the capacity as a function of number of layers laid down for a cell in which the B layer showed the highest value for capacity, and which otherwise behaved normally. There is shown on the same plot, in broken line, the capacity-layers curve for a cell in which a peak of capacity occurred at the BAB reading. It will be noticed that the curve is subsequently divergent from the typical one, which it, however, approaches as the number of layers mounts. The interpretation of this situation will be presented later.

Work is in progress on this problem, and it is hoped soon to publish more detailed results and interpretation.

TRANSLOCATION IN RELATION TO MOSAIC FORMATION IN MAIZE

By Donald F. Jones

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Communicated March 28, 1938

Paired changes in the developing endosperm of maize seeds show clearly that these alterations are not due to gene mutation or loss but to an unequal mitosis of such a nature that dominant genes are removed from one daughter cell and increased in the other. This inequality in somatic cell division may be brought about by crossing over in a multiple strand stage or by some form of segmental shift or interchange between homologous or non-homologous chromosomes.

The possibility of somatic crossing over in maize was looked for in the following way. Plants of the composition *C wx*, both on chromosome 9, were pollinated by plants having *c Wx*. The resulting triploid tissue in the endosperm had the genetic composition of *C C c Wx wx wx*. Shifts of the dominant *C* were expected to show as paired light and dark spots. In 903 seeds examined 113 light spots were found some of which were clearly paired with areas darker than normal. These seeds were cut with a file and stained with iodine. If there had been an exchange of segments between chromatids of homologous chromosomes the dark part of these aleurone twin spots should be underlaid with waxy tissue staining red in contrast to the blue-staining normal starch whenever the segment exchanged included both *C* and *wx*. Previous examination of similar mosaic areas has shown the removal of both of these linked genes in about half

of the cases. In all of the seeds examined no waxy tissue was found coinciding with the dark aleurone part of the twin spot This indicates that either the *C wx* segment was lost or exchanged with some other non-homologous chromosome.

Genetic evidence previously given indicates that there is an interchange between non-homologous chromosomes in the endosperm tissue of maize (Jones, 1937). This reciprocal exchange is shown by paired spots, one part of which exhibits the loss of one dominant gene, the other and adjoining part exhibits the loss of another dominant gene, the two genes located on different chromosomes, but both removed simultaneously. This result could be brought about either by a reciprocal translocation or by a transposition of one part of a chromosome to another followed by the loss of the augmented chromosome. In a few cases there is evidence to show that the gene removed from one daughter cell is added to the other and the reverse, that is, a reciprocal interchange.

By using genes in different chromosomes that are easily followed in somatic cells the following additional results were obtained in one family having 1076 seeds grown without any treatment to produce aberrations.

GENES USED AS MARKERS		NUMBER AND CHARACTER OF SPOTS SHOWING REMOVAL OR EXCHANGE OF		
FIRST	SECOND	FIRST GENE	SECOND GENE	BOTH GENES
C	*Pr*	270 White	170 Red	6 White and Red
C	*Su*	270 White	21 Sugary	1 White and Sugary
Pr	*Su*	170 Red	21 Sugary	0 Red and Sugary

The mosaics showing removal or exchange of both genes are paired, adjacent areas each part of which exhibits the action of the recessive allele of the gene stated. In the one white and sugary paired spot found the sugary area underlaid a dark aleurone area of similar outline. The colorless area was underlaid by waxy endosperm. This shows that a segment of the left arm of the number 9 chromosome containing *C* and *Wx* was exchanged for a segment of the right arm of the number 4 chromosome containing *Su*. In many of the red and white paired spots the red area has a darker color than the unpaired red spots on the same seeds. This indicates that there has been an exchange of *C* and *Pr* and not a loss of both in adjacent cells.

The genes used are: *C c* determining aleurone color; *Pr pr* differentiating between purple and red; and *Su su* controlling the conversion of sugar into starch. The removal of any one of these dominant genes, if present singly, can be detected in small areas, in many cases in single cells. The *su* tissue in small areas can be seen only after cutting and staining with iodine.

Taking all the data so far obtained, including mosaics in which these genes are involved, the following results are tabulated:

GENES USED AS MARKERS		NUMBER AND CHARACTER OF SPOTS SHOWING REMOVAL OR EXCHANGE OF		
FIRST	SECOND	FIRST GENE	SECOND GENE	BOTH GENES
C	*Pr*	9627 White	1571 Red	54 White and Red
C	*Su*	270 White	21 Sugary	1 White and Sugary
Pr	*Su*	929 Red	100 Sugary	0 Red and Sugary

These results are combined from many families and all three genes were not heterozygous in all of them. But the ratio of single losses to double gene exchanges or losses in paired areas can be compared and this ratio derived from the above figures is as follows:

C	*Pr*	*C Pr*
178	29	1
C	*Su*	*C Su*
270	21	1
Pr	*Su*	*Pr Su*
186	20	0

The number of somatic changes involving a single gene as listed include both paired and unpaired changes of that gene. Both *C* and *Pr* produce dark areas when present in increased numbers but whether paired or not each mosaic results from a removal of a gene from one cell. Comparing the frequency of single gene removals in the same individuals we see that *C* is taken out about 6 times as frequently as *Pr* and about 13 times as frequently as *Su*. *Pr* is lost about 9 times more often than *Su*. But the ratio of simultaneous losses of two genes in different chromosomes to the separate losses of the individual genes involved is more nearly constant.

In this triploid tissue there are 30 somatic chromosomes. Presumably segmental interchange may take place between either arm of any two chromosomes. If this exchange takes place at random 1 in 58 mosaic areas would be expected to show the removal of any two heterozygous genes in different chromosomes. The result would be paired mosaics showing the action of recessive genes in approximately equal and adjoining areas. Any exchange that does not include both genes would be classed as a single mosaic. The relative frequency of single mosaics is determined possibly by the position of the gene on the chromosome. In the three inter-chromosomal gene pairs considered, one gene is removed more frequently than the other. Therefore it would be expected that the ratio of paired losses to single losses would be less than 1 to 58 for one gene and more than 1 to 58 for the other. This is in agreement with the observed results in two of the three cases shown.

No paired losses of *Pr* and *Su* were found in this untreated material. In seeds x-rayed shortly after fertilization 15 such mosaic areas were noted in 560 seeds examined. In the treated material the single gene losses

were so numerous and complex in outline that no comparative counts could be made. Since no *Pr Su* paired mosaic areas were observed in 4117 untreated seeds examined where at least 5 were expected they may have been overlooked.

That these gene shifts occur simultaneously is shown by the fact that the paired areas are approximately equal in area and outline and in a few cases have been seen to include only two cells. In several instances multiple changes have been found showing three or more adjoining areas of approximately equal size. Some of these triple spots are red, white and dark; sugary, white and dark; and light, white and dark. In these cases either more than two chromosomes are involved or additional changes occur at subsequent cell divisions. The exact nature of these changes cannot be determined at present but the cytological possibilities have been outlined by Dubinin and Khvostova (1935).

Paired and unpaired colorless and dark areas occur on the same seeds heterozygous for the *C* aleurone color gene. Either a piece of a chromosome is lost or the daughter cell that receives the extra *C* gene is nonviable, or grows in such a manner that the resulting tissue does not reach the surface where it can produce color while the other daughter cell lacking *C* does reach the surface. By following the linked waxy gene in the endosperm it is possible to demonstrate that this is the situation in a few cases but it does not seem likely that this can be the explanation for all unpaired mosaics, since unpaired dark areas are much less frequent than unpaired colorless. There is also no reason to expect cells that have received an additional dominant gene are less viable than cells that have received an extra recessive gene. Since deletions have been demonstrated cytologically to be of frequent occurrence in maize there is now good evidence to show that both deletion and translocation result in somatic changes.

If translocation takes place at random, as the evidence presented here indicates, then it would be expected to take place between homologous chromosomes as a chance recombination and in a few cases at or near homologous loci. If, in some diploid organisms, only these homologous exchanges result in viable cells or cells that are not handicapped in development the surviving visible changes would be the result of a process that simulates somatic crossing over but in reality is different from the exchange that normally takes place at germ cell formation.

Dubinin, N. P. and V. V. Khvostova, "The Mechanism of the Occurrence of Complex Chromosome Rearrangements," *Jour. Biologie*, **4**, 935–975 (1935).

Jones, D. F., "Somatic Segregation and Its Relation to Atypical Growth," *Genet.*, **22**, 484–522 (1937).

NOTE ON ESTIMATING BACTERIAL POPULATIONS BY THE DILUTION METHOD

By Robert Dean Gordon

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Communicated March 17, 1938

One method of obtaining an estimate of bacterial density in a solution, is to inoculate 1-ml. portions of the solution into each of several test tubes containing sterile nutrient medium; then dilute the solution in a convenient ratio and inoculate several more test tubes with 1-ml. portions, then dilute again, and so on, for several successive dilutions. After a period of incubation, the proportions of "positives" (tubes showing growth) obtained from each of the several dilutions, are taken as indications of the density of "viable" bacteria in the original solution.

In 1933 Halvorson and Ziegler[1] published a set of tables, in which they assumed the dilution ratio to be 10:1, and supposed a total of thirty test tubes to be inoculated with three successive dilutions, ten with one dilution, ten with a 10-fold greater dilution and ten with a 100-fold greater dilution than the first. If respectively p_1, p_2 and p_3 tubes, out of the ten inoculated, show growth, their tables show a corresponding estimate of the mean density of viable bacteria in the middle dilution. For more details, their booklet[1] may be consulted.

Dr. C. E. ZoBell, of the Scripps Institution of Oceanography, in experimenting with these tables found them to be unsatisfactory and unreliable, and asked the writer to examine them. It was found that the estimates were obtained in accordance with R. A. Fisher's "criterion of maximum likelihood," which is shown to be of very questionable significance in this type of problem. In the Bayes-Laplace theory of inverse probability the estimates are modal values. Since the estimates are actually stated as three figure numbers (e.g., 2.53/ml., 43,500/ml., etc.), it seems evident that the most reasonable simple type of estimate is the *geometric mean*. The writer has developed formulas to obtain this value together with formulas for the standard deviation of its logarithm, to serve as an indication of its proportionate accuracy. It is expected to simplify these formulas to a greater degree than at present, but they are now in form which can be used for computation.

The notation of the writer is not the same as that of Halvorson and Ziegler. It is as follows:

n_{10} = number of test tubes showing growth, out of the ten inoculated with the highest concentration of the solution.

n_1 = number of test tubes showing growth, out of the ten inoculated with the middle dilution.

$n_{0.1}$ = number of test tubes showing growth, out of the ten inoculated with the highest (100-fold) dilution.

$\bar{\rho}$ = geometric mean estimate of the density of viable bacteria in the solution, corresponding to the middle dilution (i.e., to n_1).

x = an integer $\geqq x_0$ where $x_0 = 1110 - 100n_{10} - 10n_1 - n_{0.1}$.

$N = n_{10} + n_1 + n_{0.1}$.

γ = "digamma 1" = $-0.577216\ldots$.

γ' = "trigamma 1" = $+1.644934\ldots$.

$\log_e 10 = 2.302585\ldots$.

Δ = Boolean difference operator; operates on x.

H_0 = operator on x_0.

$= (1 + E + \ldots + E^{99})^{n_{10}}(1 + E + \ldots + E^{9})^{n_1}$

where E = Boolean operator $= (1 + \Delta)$;

$= 1 + P_1E + P_2E^2 + \ldots + P_rE^r$.

With this notation, the following formulae hold:[2]

$$\log_e\bar{\rho} = \gamma + \log_e 10 - \frac{H_0\Delta^N\left\{\frac{\log_e x_0}{x_0}\right\}}{H_0\Delta^N\left\{\frac{1}{x_0}\right\}}. \tag{13}$$

$$\sigma^2_{\log_e\rho} = -(\log_e\bar{\rho})^2 + [\gamma + \log_e 10]^2 + \gamma' - 2[\gamma + \log_e 10]\cdot\frac{H_0\Delta^N\left\{\frac{\log_e x_0}{x_0}\right\}}{H_0\Delta^N\left\{\frac{1}{x_0}\right\}} + \cdot + \frac{H_0\Delta^N\left\{\frac{(\log_e x_0)^2}{x_0}\right\}}{H_0\Delta^N\left\{\frac{1}{x_0}\right\}}. \tag{16}$$

For use in these formulas, the following auxiliary formulas have been obtained:

$$(-1)^N\Delta^N\left\{\frac{1}{x}\right\} = \frac{N!(x-1)!}{(x+N)!}. \tag{19}$$

$$(-1)^N\Delta^N\left\{\frac{\log_e x}{x}\right\} = \frac{N!(x-1)!}{(x+N)!}\log_e x + \sum_{p=N}^{\infty}\frac{(-1)^{p-N+1}}{x^{p+1}}\cdot\frac{p!}{p-N!}\cdot\left(1 + \frac{1}{2} + \frac{1}{3} + \ldots + \frac{1}{p}\right)B_p^{(-N)}{}_N. \tag{21}$$

$$(-1)^N \Delta^N \left\{ \frac{\log_e x}{x} \right\} = \frac{N!(x-1)!}{(x+N)!} \log_e(x+N) \qquad (21a)$$

$$- \sum_{p=N}^{\infty} \frac{1}{(x+N)^{p+1}} \cdot \frac{p!}{(p-N)!} \left((1 + \frac{1}{2} + \frac{1}{3} + \ldots + \frac{1}{p} \right) B_{p-N}^{(-N)}$$

where $B_{p-N}^{(-N)}$ are Bernoulli numbers of degree $p - N$ and order $(-N)$; cf., L. M. Milne-Thompson, "Calculus of Finite Differences" (1933), page 129. We have tabulated most of these numbers which we need.

For the coefficients P_ν of the operator

$$H_0 = 1 + P_1 E + P_2 E^2 + \ldots + P_\nu E^\nu + \ldots .$$

we have the direct formula

$$P_\nu = \sum_{r=0}^{.01\nu} \sum_{s=0}^{.10-10r} (-1)^{r+s} \, C_r^{n_{10}} \, C_s^{n_1} \, C_{\nu-100r-10s}^{\nu-100r-10s+n_{10}+n_1-1} \qquad (30)$$

where C_a^b is the binomial coefficient. Also

$$P_{99n_{10}+9n_1-\nu} = P_\nu .$$

For intermediate values of the subscript ν, P_ν is given by an Hermite expansion

$$P_\nu = \left[\left(\sum_{\mu=0}^{\infty} A_{2\mu} \cdot \frac{d^{2\mu}}{d\xi^{2\mu}} \right) \frac{c}{\sqrt{\pi}} \, e^{-c^2(\xi-b)^2} \right]_{\xi=\nu} \qquad (33)$$

where $b = \frac{1}{2}(99n_{10} + 9n_1)$ and $c^2 = \dfrac{6}{9999n_{10} + 99n_1 + 2}$

and the first few coefficients $A_{2\mu}$ have the following values:

$$A_0 = 10^{2n_{10}+n_1}$$

$$A_2 = 0 \qquad (38)$$

$$A_4 = -\frac{10^{2n_{10}+n_1}[(10^8-1)n_{10} + (10^4-1)n_1 + 2]}{2880}$$

and

$$A_6 = 10^{2n_{10}+n_1} K_6$$

$$A_8 = 10^{2n_{10}+n_1} \left[K_8 + \frac{1}{2} K_4^2 \right]$$

. . . . . .

where

$$K_{2\mu} = \frac{B_{2\mu}}{(2\mu)(2\mu)!}\,[(100^{2\mu} - 1)n_{10} + (10^{2\mu} - 1)n_1 + 2]$$

and $B_{2\mu}$ is the Bernoulli number of first order, of degree 2μ (cf. Milne-Thompson, l. c.). A trigonometric (Fourier) expansion is also possible for P_ν, and may prove more useful.

Mrs. Naomi Lancaster has used these formulas to make several computations of $\bar{\rho}$, shown in the following table and compared with the corresponding estimates of Halvorson and Ziegler:

ARGUMENTS			$\bar{\rho}$ COMPUTED BY US	$\bar{\rho}$ FROM HALVORSON AND ZIEGLER	% DEVIATION FROM HALVORSON AND ZIEGLER
n_{10}	n_1	$n_{0.1}$			
10	7	3	1.43	1.53	−7.0
8	5	1	0.291	0.267	+9.0
4	2	1	0.086	0.080	+7.5

The per cent deviations shown would appear to be significant in bacteriological work. For instance, if a bacteriologist desires to attribute a particular degree of certainty to the proposition that his estimate is within 20% of the true value, the knowledge that his method of arriving at the estimate could account for a bias of from 7 to 9% must certainly be of significance to him.

As a matter of fact, comparisons of direct plate counts with estimates from Halvorson and Ziegler's tables, on the same materials, corroborate the above theoretical comparisons and even indicate that in other parts of the tables, the bias may be considerably more serious.

In order to put these results into practical form for bacteriologists and others, as well as to test the theory experimentally, it would be necessary to compute tables to replace those of Halvorson and Ziegler,[1] which would require a considerable financial outlay.

* Contributions from the Scripps Institution of Oceanography. New Series No. 18.

[1] Halvorson and Ziegler, *Quantitative Bacteriology*, Burgess Publishing Co., Minneapolis, Minnesota (1933).

[2] A complete discussion will be published elsewhere.

TEMPERATURE AND THE CRITICAL INTENSITY FOR RESPONSE TO VISUAL FLICKER

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Communicated March 24, 1938

1. The investigation of the properties of the flicker-response contour for visual excitation[1] has involved the measurement of the inter-dependence of flash-frequency F and intensity I in a flash at the critical point for reaction signifying "recognition" of flicker. It has been shown that with very different animals there obtain relations of invariant fundamental form[2] between F and I, the area of receptor surface involved,[3] the proportion of light-time to dark-time in the flash cycle,[4] and the temperature[5] of the organism. The dynamical properties of these relationships are therefore non-specific,[6] as indeed they are for other modes and types of intensive discrimination as well.[15] They are not determined by morphological characteristics of the animal as a whole,[1] nor of its peripheral receptor organs (save in minor respects not pertinent to this discussion[7]).

The one feature common to the responses concerned is their dependence upon the activity of a population of neural effects. It accords with this that a probability integral[8] accurately describes the connection between F and $\log I$. The numerical values of the parameters of the integral are determined by the (genetic) constitution of the organism[9], but its nature as a summation of a particular kind of probability distribution is nonspecific.

2. It is impossible to reconcile these facts, and the related phenomena of intensity discrimination in general, with the hypothesis[10] that the properties of the flicker-response curve are determined by the photochemical excitability of the retina.[11] The parameters of the probability summation, or the parameters of any arbitrary descriptive curve which might be used, do not have the behavior required by that conception.

It is important, however, to determine what quantitative properties these parameters do exhibit. The theoretical background of the application of a probability integral to a case of this kind involves the assumption[12] that the summated neural effects appealed to are the products of elements which in time *fluctuate* in their capacity to contribute to the production of the result used as an end-point (i.e., response). On this basis the measured relationships between F_m and σ_F[13], I_m and σ_I[14], ΔI_m and $\sigma_{\Delta I}$[15], etc., as functions of temperature, area, and t_L/t_D, have been extensively explored, with demonstration of their rational coherence. This is also the case with the curiously different effects of altering temperature, area and t_L/t_D, so far as the qualitative properties of the parameters of the probability integral are concerned and as regards their quantitative features[16]

when t_L/t_D is used as an independent variable. It was at first supposed[17] that response to flicker should be so complexly determined that the data on the $F - \log I$ curve at various temperatures could not reasonably be expected to submit to simple formulation. In particular, it was suspected that the application of the activation-energy equation (Arrhenius) would not be found to yield a constant value of the "temperature characteristic."[18] (This would not of itself preclude rational analysis, as I have recently shown[19] for another case.)

In discussing the relation between flash frequency (F) and critical intensity (I) for reaction to visual flicker,[17] under the conditions imposed by work with lower animals, we stressed the fact that for an insect (larva of *Anax*) and a vertebrate (the sunfish *Enneacanthus*) there did not appear to obtain a simple quantitative relationship between temperature and critical intensity at fixed flash-frequency. The observations were made at only three temperatures, however, and later work has led to an amplification and correction of the earlier conclusion. The effect of changing the temperature is simple enough, since it leads merely to a shift of the position of the $F - \log I$ curve on the $\log I$ axis, without changing its form or altering the maximum to which the curve rises.[17] So many instances occur in which the magnitudes of events in biological systems are differently related to temperature on either side of a critical temperature[20] that we should have been on our guard against its happening with flicker excitations also. Where it does occur, observations at a number of temperatures are of course required to detect it.

The $F - \log I_m$ contour for the turtle *Pseudemys* is a single sigmoid curve,[21] and not, as with other vertebrates thus far tested,[1] a complex of two (or three)[22] parts This is in keeping with the fact that its retina apparently contains no rods, but only sensory cells of a single type, cones. It should thus provide a somewhat simpler condition for analysis of the properties of the flicker-response curve as a function of temperature.

3. As with *Anax* and *Enneacanthus*, we find that the *shape* of the $F - \log I$ curve for *Pseudemys* is not affected by change of temperature. With increase of temperature the whole curve is merely moved to lower intensities. The bearing of this shift upon certain theories of the meaning of the flicker curve we have commented upon previously.[17] The curve is well described by a probability integral in $\log I$.[21] Its maximum is independent of temperature, and so is its $\sigma_{\log I}$, but the abscissa of its inflection point (τ') decreases with rise of temperature (Fig. 1).

4. From data on the measurement of I_m at any fixed flash-frequency we can then estimate the dependence of a single parameter, τ', upon the temperature. Experiments were made at $F = 20$, and $F = 30$, the inflection point falling between them We take $1/I_m$ as a measure of excitability, with F constant. Reasons outside the immediate considerations of

flicker phenomena also lead to this procedure.[22] The excitability, in terms of marginal response to flicker, is increased with rise of temperature. Figure 2 shows that the rate of increase obeys the Arrhenius equation, with a critical temperature at 30° or a little below. The values of the temperature characteristic μ are 27,000± (up to) 30° and 12,000+ (beyond 30°).

5. There are reasons for assuming that some rather direct function of the critical intensity for marginal response to flicker is a measure of the

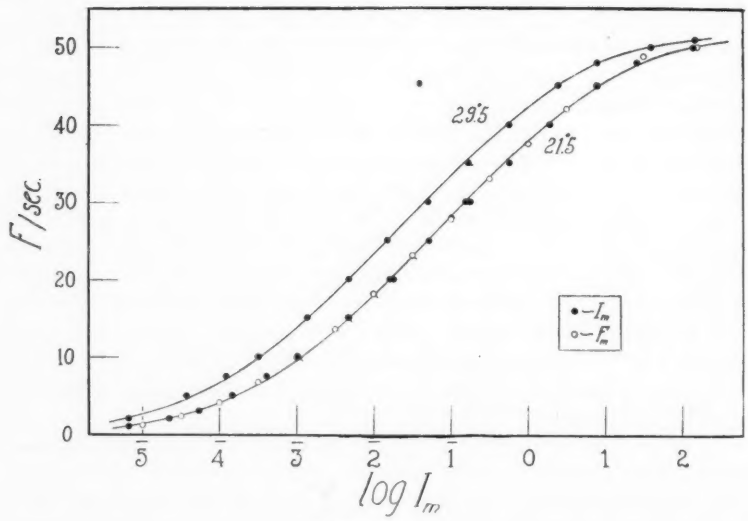

FIGURE 1

Mean critical flash illumination $t_L/t_D = 1$ for response of the turtle *Pseudemys* to visual flicker, as a function of flash-frequency F, at two temperatures. Each point is the mean[1] of three observations on each of the same ten individuals at every point. (Double determinations bear tags.) The curve is the same probability integral drawn through each series, with shift of the inflection point to the left with rise of temperature.

"driving force" responsible for the reaction. We have pointed out[1] that the relation of I_m to its variations (P.E.$_I$ or σ_I) is precisely that encountered in studies of the behavior of σ_R, where R is the *rate* or *frequency* of a biological phenomenon as a function of temperature.[23] An essential fact is that the relative variation of I is constant (independent of temperature), so that σ_I/I (or $\sigma_{(1/I)}/1/I$) is constant. The rate or frequency (as, of the heart beat) has been taken to be proportional to the velocity of a controlling chemical change. The reasons for this are (1) that it obeys the work function and (2) with a value of the "activation energy" (μ) which falls

within the range characteristic for chemical processes proceeding at ordinary temperatures. On this basis $1/I_m$ for reaction of *Pseudemys* to flicker (at fixed F) is determined by the velocity of a system of chemical transformations of which the slow member is one having $\mu = 27{,}000\pm$ below 30° and $\mu = 12{,}000+$ above 30°.

The obvious way in which to account for such facts is through the supposition that excitability with respect to the recognition of flicker (measured by $1/I$) is governed by the velocity of a terminal reaction affecting all the nervous elements implicated in the determination of the index

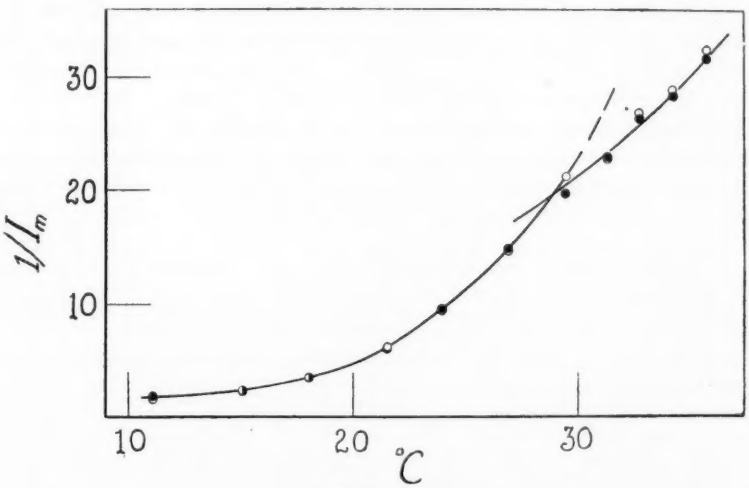

FIGURE 2

The excitability for response to flicker, measured by the reciprocal of the critical flash intensity, at fixed flash frequency, increases with temperature according to the Arrhenius equation, with a critical temperature at 30°−. Observations at $F = 20$ and at $F = 30$ are brought together for comparison by multiplying those at $F = 30$ by a constant (10.21).

response, and that the speed of this terminal reaction is controlled by a chain of reactions including at least two steps. One of these steps is characterized by $\mu = 27{,}000$, the other by $\mu = 12{,}400$.

The existence of such steps has been referred to[24] in terms of a catenary series. The unwarranted and irrelevant assumption has been made by some[25] that the links in such a chain should be, or were supposed to be, related in a mass-action sequence. The evidence has on the contrary[26] long required that the interconnection of the steps be in terms of catalyzed reactions, one of which "releases" the next with a frequency depending on

the speed of the first reaction. In such a chain (*a*) the frequency of occurrence of the end result depends on the slowest individual step in the chain and (*b*) the occurrence of specific, sharp critical temperatures may be rationally accounted for by the nature of the system in which these processes occur.[26] The association of sets of values of μ in connection with a particular phenomenon[24] is then reasonable if one assumes a specific organization of different catenary sets of processes in diverse situations. A mechanism for the integration of such sets of reactions in terms of the properties of catalytic surfaces remains to be more fully developed; this mechanism must of course account for the fact that critical temperatures in general are distributed in such a way as to occur predominantly at definite places on the temperature scale.[24] The 30° point encountered in the present experiments is one of these. The dynamics of the situation here conceived can be explored in several ways. Experiments to be described subsequently permit a decision as to whether the shift of μ at a critical temperature is due (*a*) to a modification of relations within a system of contact-catalysis processes, or (*b*) to the "injury" of a certain number of the "elements" defined by the foregoing analysis.[27]

[1] *Jour. Gen. Physiol.*, **19, 20, 21,** (1935–38).

[2] Crozier, W. J., *Proc. Nat. Acad. Sci.*, **23,** 71 (1937).

Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **21,** 223, 17 (1937–38); *Proc. Nat. Acad. Sci.*, **23,** 516 (1937).

[3] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **21,** 223 (1937–38).

[4] *Ibid.*, **21,** 313 (1937–38).

[5] *Ibid.*, **20,** 393, 411 (1936–37); and material in course of publication.

[6] *Proc. Nat. Acad. Sci.*, **23,** 71; *J. Gen. Physiol.*, **20,** 393; 411; **21,** 17, 203.

[7] *Ibid.*, **20,** 363 (1936–37); **21,** 223 (1937–38); (in press).

[8] *Proc. Nat. Acad. Sci.*, **23,** 71 (1937); *Jour. Gen. Physiol.*, **21,** 17, 313 (1937–38).

[9] *Proc. Nat. Acad. Sci.*, **23,** 516.

[10] Hecht, S., *Physiol. Rev.*, **17,** 239 (1937).

[11] *Jour. Gen. Physiol.*, **20,** 393, 411 (1936–37); **21,** 313; (in press) (1937–38).

[12] *Proc. Nat. Acad. Sci.*. **23,** 71 (1937).

[13] *Jour. Gen. Physiol.*, **20,** 211, 363; **21,** 17, etc.

[14] *Proc. Nat. Acad. Sci.*, **22,** 412 (1936); and footnote 1.

[15] *Ibid.*, **22,** 412 (1936); Crozier, W. J., and Holway, A. H., *Ibid.*, **23,** 23 (1937); Holway, A. H., and Crozier, W. J., *Ibid.*, 509 (1937).

[16] *Jour. Gen Physiol.*, **21,** 313 (1937–38); (in press).

[17] *Ibid.*, **20,** 393, 411 (1936–37).

[18] *Ibid.*, **7,** 189 (1924–25).

[19] Cf. Crozier, W. J. (in press) and *Jour. Gen. Physiol.*, **7,** 189 (1924–25).

[20] *Ibid.*, **7,** 189 (1924–25); **9,** 525 (1925–26).

[21] *Proc. Nat. Acad. Sci.* (in press).

[22] (*Triturus*) (in press).

[23] Crozier, W. J., *Détérminisme et variabilité*, Paris: Hermann, pp. 56 (1935).

[24] *Jour. Gen. Physiol.*, **7,** 189, 429 (1924–25), etc.

[25] Burton, A. C., *Jour. Cell. Comp. Physiol.*, **9**, 1 (1936); see Hoagland, H., *Ibid.*, **10**, 29 (1937).

[26] *Jour. Gen. Physiol.* **9**, 525, 531 (1925–26); **18**, 801 (1934–35), etc.

[27] The thermostat employed in these experiments (cf. Stier, T. J. B., and Crozier, W. J., 1932–33, *Jour. Gen. Physiol.*, **16**, 757) was constructed with aid from a grant by the Elizabeth Thompson Science Fund to one of us, which is gratefully acknowledged.

SPECIFIC CONSTANTS FOR VISUAL EXCITATION. II

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Communicated March 24, 1938

I. In previous communications we have dealt with considerations arising from measurements of the flicker-response contours for fishes of different types, which can in certain cases[1] be subjected to genetic tests. The curves describing the relationship between flash-frequency F and flash-intensity I for various teleosts[2] are of specific form: their rod-excitation and cone-excitation parts are described with excellent fidelity by probability integrals (F vs. log I), and the parameters of this formulation exhibit significant differences according to the kind of teleost concerned. These parameters ($F_{max.}$; log I at inflection; and $\sigma_{\log I}$) show properties in relation to various experimental variables which justify the use of the conception that a probability formulation is applicable to the data of response to visual flicker.[3]

II. Evidence has been provided[2] showing that the quantitative values of these parameters are dependent upon the genetic constitution of the organism.[2] A test of this position, and at the same time a check upon the possible rôle of certain physiological factors which should be irrelevant if our view is correct, is provided by the determination of the $F - \log I$ curve for individuals in which an albino mutation has occurred. The test is of additional interest with respect to the significance of retinal pigmentation and of the significance of the iris of the eye.

With reference to the latter point, it could be supposed that certain quantitative properties of the $F - \log I$ curve (e.g., τ', the abscissa of inflection) could be a function of the iris aperture, and of the translucency of the iris and ocular media. We have found no reason whatever for supposing that this is a real consideration, since the shape of the $F - \log I$ curve in neither fishes,[2] amphibian,[4] turtle[5] nor man[6] gives any indication that it need be taken into account. It could also be supposed that in the absence of retinal melanin the relative flicker-response performance of rods and of cones could be modified in other ways. The fact that visual per-

formance curves for albino animals have not in any instance (human or otherwise)[13] been reported upon in detail lends added importance to such observations.

The significance of an examination of this kind is of several sorts: (1) If the $F - \log I$ curve is unaltered by the albinistic state, it is shown (*a*) that a mutation not primarily concerned with the nature of the elements of excitability[7] defined by the properties of the $F - \log I$ curve does not affect

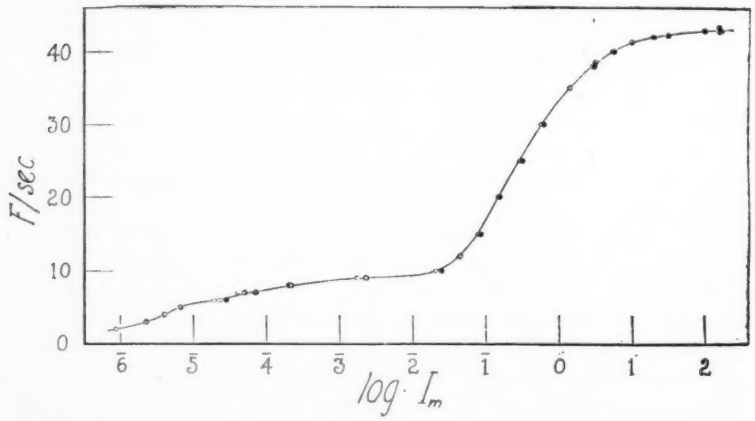

FIGURE 1

Log mean critical illumination (I_m) as a function of flash-frequency F for the teleost *Xiphophorus helleri:* open circlets, based on 30 observations (10 individuals) of normal "wild type" as described in an earlier report;[11] solid circlets and half shaded, data on three albino mutants of this stock (three observations on each at every point); 21.5°C. The "cone" curve (cf.[2]) for the albinos is possibly a very little beyond that for the wild type, but this is not significant. The curve drawn is the theoretically analyzed curve for the wild type.[2] The new data show in the zone of overlap of "rod" and "cone" contributions the kind of scatter discussed[6] for the measurements with normal *Xiphophorus*. The half-shaded circlets are determinations of F_m at fixed levels of I (cf.[3]), made to determine if for the albino individuals the curve at high intensities turns downward, as could be expected (from analogy with human data) if "glare" is an especially significant factor.

the objective measures of these properties, and (*b*) that melanin in iris and retina has no influence upon the $F - \log I$ curve. (2) If the curves for albino individuals should differ significantly from those of the parent stock, an interesting opportunity would be presented for further analysis.

A test of this kind has been possible with individuals of *Xiphophorus helleri*, the well-known viviparous aquarium fish. We are under obligation to Dr. C. P. Haskins of this Laboratory for the opportunity to utilize albino individuals derived from his cultures.

III. A curve of performance with respect to critical flash-illumination as a function of flash frequency has already been published[8] for *Xiphophorus helleri*. Corresponding determinations were made with individuals arising in the same stock which were to careful inspection completely lacking in melanin, in retina and elsewhere. Three individuals (1 ♂, 2 ♀) were available for a complete series of tests.

In figure 1 it is seen that over the entire range of explorable intensities the correspondence of the measurements in the two series, normal and albino, is essentially complete. There were certain grounds for expecting that at high intensities the curve might show negative slope[9] for the albinos, but this has not been found. The data supply a striking instance of the reproduceability of the $F - \log I$ curve. The variation of $\log I_c$ (Fig. 2.) follows the rule already found for flicker response in general,[10] and shows quantitative agreement with the values gotten for non-albino individuals of this stock of *Xiphophorus*.[11] We have already shown that certain other genetic color differences have no influence upon the $F - \log I$ curve, but (in other genera) may influence the variability function.

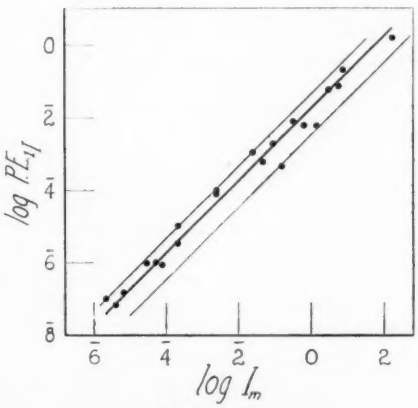

FIGURE 2

The *scatter* of the individual measurements of critical flash-intensity, as related to I_m, for reaction to flicker at various flash frequencies for albino *Xiphophorus helleri*. The central line drawn for *mean* $P.E_{1/I_1}$ divides the observations equally (cf.[12]). Its slope = 1, and its position is identical with that previously obtained[8] for normal *Xiphophorus*. The *breadth* of the band ($= k^{\sigma}{}_{\sigma\sigma}$) agrees quantitatively with that previously observed when correction is made for the fact that three individuals are involved in the present instance (albinos) and ten in the earlier series[8] (normals).

IV. *Summary.*—Albino individuals, mutationally arising in a stock of the teleost *Xiphophorus helleri*, show precisely the same values of critical flash illumination for response to flicker as do normal individuals of the same stock. This shows (1) that retinal pigmentation (and iris pigment) has no influence upon the quantitative performance of the implicated elements of visual excitability; and (2) that, in the absence of such superimposed influences, the $F - \log I$ curves are highly reproduceable characteristics of the composition of the organism.

[1] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Proc. Nat. Acad. Sci.*, **23**, 516 (1937); *Jour. Gen. Physiol.*, **21**, 17 (1937–38).

[2] Wolf, E., and Zerrhan-Wolf, G., *Jour. Gen. Physiol.*, **19**, 459 (1935–36); Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Ibid.*, **20**, 211, 411 (1935–36); **21**, 17; *Jour. Exptl. Zoöl.* (in press).

[3] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **21**, 223; 313 (1937–38); (in press); **20**, 393, 411; *Proc. Nat. Acad. Sci.* (in press).

[4] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Exptl. Zoöl.* (in press).

[5] *Jour. Gen. Physiol.* (in press).

[6] Crozier, W. J., *Proc. Nat. Acad. Sci.*, **23**, 71 (1937); Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **21**, 203 (1937–38).

[7] Crozier, W. J., *Proc. Nat. Acad. Sci.*, **23**, 71 (1937).

Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Ibid.*, **23**, 516 (1937); *Jour. Gen. Physiol.*, **21**, 17 (1937–38).

[8] *Ibid.*, **21**, 17 (1937–38); *Proc. Nat. Acad. Sci.*, **23**, 516 (1937).

[9] *Jour. Gen. Physiol.*, **20**, 211, 411 (1935–36).

[10] Crozier, W. J., *Ibid.*, **19**, 503 (1935–36); and footnotes [2] and [3].

[11] *Jour. Gen. Physiol.*, **21**, 17(1963–37).

[12] Crozier, W. J., and Holway, A. H., *Proc. Nat. Acad. Sci.*, **23**, 23 (1937).

[13] Since this was written we have learned of a recent publication by Bunge, E., and Heyn, W., *Klin. Monatsbe. Augenheick.*, **100**, 178, 1938, in which the dark adaptation curve for a human albino is shown not to differ from the normal.

THE RELATIONS BETWEEN STEFAN'S RADIATION LAW, NERNST'S HEAT THEOREM AND MAXWELL'S FORMULA FOR THE RADIATION PRESSURE

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Communicated April 15, 1938

Boltzmann, as is well known, derived Stefan's law of radiation by combining the first and second laws of heat with Maxwell's formula for the radiation pressure. On the other hand, the statement is often found that on the basis of thermodynamical relations, the empirical confirmation of Stefan's law represents at the same time an empirical confirmation of Maxwell's expression for the radiation pressure. As will be shown in the following, such a reasoning fails to be conclusive, for only by taking into account Nernst's heat theorem in Planck's formulation are we led to Maxwell's relation for the radiation pressure. Conversely, however, Stefan's law and Maxwell's formula, by their combination with the first and second laws of thermodynamics, yield Nernst's heat theorem for the special case of the black body radiation. It will be the task of the following axiomatic investigation to prove this and thus, for the special case of the

black body radiation, to determine the arbitrary functions and constants which occur in "classical" thermodynamics, based on the first and second laws.[1]

We start with the energy equation of classical thermodynamics. It holds for all cases in which the state of a system is completely determined by temperature and volume, and a normal uniform pressure is the only force acting upon the system. For such cases the combination of the first and second laws yields the energy equation in the following form[2]

$$(\partial U/\partial V)_T = T\,(\partial p/\partial T)_V - p \tag{1}$$

where U, V, T and p denote the internal energy, the volume, the absolute temperature and the pressure, respectively.

If U be known as a function of T and V, we obtain p as a function of T and V, and thus the equation of state by integrating (1), a partial differential equation of the first order with respect to T. We find

$$p = T \int_0^T \left(\frac{\partial U}{\partial V}\right)_T \frac{dT}{T^2} + Tf(V). \tag{2}$$

Here $f(V)$ is an arbitrary function of the volume, for the determination of which the first and second laws alone do not suffice. From the relation which represents the internal energy as a function of V and T, the equation of state of the system can thus only be derived to within an arbitrary function of the volume which is to be multiplied by the temperature.

If, on the other hand, the equation of state be given, i.e., $p = f(V, T)$, the internal energy may be derived from (1) by integrating with respect to the volume, or

$$U = \int_0^V [T(\partial p/\partial T)_V - p]dV + g(T) \tag{3}$$

where $g(T)$ again represents an arbitrary function of the temperature.

The relations (1), (2) and (3) are, of course, also applicable to the special case of the black body radiation. In this application, however, a peculiarity characterizing the black body radiation is of decisive importance. As is well known,[3] it follows at once from Kirchhoff's radiation law that in the case of radiation, the ratio of the internal energy to the volume is simply a function of the temperature, or

$$U(V, T) = V \cdot u(T). \tag{4}$$

Since the last term in (3) is independent of the volume, we have to put in (3), if it is applied to the special case of the black body radiation,

$$g(T) = 0. \tag{5}$$

If therefore p be given as a function of the energy density u by Maxwell's relation

$$p = u/3, \tag{6}$$

the insertion into (3) of the value of p as given by (6) leads, indeed, to a unique determination of the energy density as a function of the temperature, if we consider equations (4) and (5); we obtain Stefan's law in the form

$$u = a\,T^4, \tag{7}$$

a being an integration constant. In the usual presentations (5) is tacitly assumed, without any mention of the fact that (5) is a consequence of (4).

In reversing Boltzmann's well-known derivation of Stefan's law we may, however, also assume (7) to be given, the factor a being quite a definite constant. The combination of (2) and (7) then leads at once to the relation

$$p = \frac{1}{3}a\,T^4 + T f(V). \tag{8}$$

On the basis of this relation (7), Stefan's law, appears compatible with (6), Maxwell's formula, only if

$$f(V) = 0. \tag{9}$$

We cannot, therefore, deduce Maxwell's formula from Stefan's law by means of the first and second laws unless we can show that $f(V)$ must vanish.

Classical thermodynamics as resulting from the first and second laws does not suffice for this purpose. It proves to be necessary to take Nernst's heat theorem also into account, in Planck's form, according to which the entropy of a system must vanish in the limit for the absolute zero, or

$$\lim_{T \to 0} S = 0. \tag{10}$$

The differential of the entropy is determined by the first and second laws, in accordance with the well-known relation

$$dS = (dU + pdV)/T. \tag{11}$$

In this equation we may insert for p the value from (8), and according to (4) and (7) we may put

$$U = aVT^4. \tag{12}$$

On integrating we then find

$$S = \frac{4}{3}aVT^3 + \int f(V)\,dV + C \tag{13}$$

where C denotes an arbitrary quantity which, however, is independent of the volume.

Quite independently of Nernst's heat theorem, we may prove that the quantity C must vanish. For, according to (4) U must vanish for vanishing V; but, if C should differ from zero, then, according to (13), the entropy would also differ from zero for this case. This, however, is inconceivable since we cannot ascribe an entropy differing from zero to a system whose volume and internal energy vanish and which, therefore, is no system at all.[4] Hence, the last term in (13) must be zero, or

$$C = 0. \tag{14}$$

If, however, Nernst's heat theorem is to hold in Planck's form, $f(V)$ must also vanish. Thus (9) appears to be proved and the derivation from Stefan's law of Maxwell's formula for the radiation pressure appears to be complete.

Finally, we shall assume both Stefan's law and Maxwell's formula for the radiation pressure to be given, in combination with classical thermodynamics. Then a comparison of (6) and (8) first shows the necessity of the vanishing of $f(V)$. Furthermore, as was shown before, (14) may be gained without using Nernst's heat theorem at all. Therefore it appears to be proved on the basis of Stefan's law and the electro-magnetic formula for the radiation pressure that (10) must be fulfilled for the radiation. Thus in the special case of the black body radiation Nernst's heat theorem in Planck's formulation[5] may be deduced simply from classical thermodynamical and electrodynamical principles.

[1] A more general treatment including applications to the thermodynamics of long-chain-molecules will be given in a forthcoming paper of one of the authors (E. G.) whereas a forthcoming paper of the other author (A. E. H.) will deal with the interpretation of the thermodynamics of the black body radiation from the viewpoint of the photon theory.

[2] Cf. e.g., Mark W. Zemansky, *Heat and Thermodynamics*, p. 233 (1937).

[3] Cf. e.g., M. Planck, *Theory of Heat*, p. 193 (1932).

[4] Cf. e.g., P. S. Epstein, *Textbook of Thermodynamics*, p. 333 (1937).

[5] In Nernst's own original formulation his heat theorem simply postulated that the entropy must remain finite in the limit for $T \to 0$. This postulate is fulfilled if the specific heat at constant volume, that is

$$C_V = (\partial U/\partial T)_V$$

vanishes for $T = 0$. This consequence follows at once from Stefan's law since the differentiation of (6) with respect to the temperature yields the relation

$$C_V = 4aVT^3.$$

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